

FOSSIL FISH REMAINS FROM THE PLIOCENE KANAPOI SITE, KENYA

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ABSTRACT. Over 2,800 fossil fish elements were collected in the 1990s from the Pliocene site of Kanapoi, located in the Turkana Basin, northern Kenya. The Kanapoi fish fauna is dominated by large piscivores and medium to large molluscivores, whereas herbivorous fish are rare. The genera *Labeo*, *Hydrocynus*, and *Sindacharax* are abundant in the deposits, as are large percoids and catfish. While the Kanapoi fauna has many similarities with both the near-contemporaneous fauna recovered from the Muruogori Member at nearby Lothagam and the site of Ekora, including the extinct genera *Sindacharax* and *Semlikiichthys*, it differs significantly in two features. The Kanapoi fauna is dominated by a *Sindacharax* species that is absent at Muruogori and it lacks two other *Sindacharax* and two *Tetraodon* species which are common in the Muruogori deposits and at Ekora. The Kanapoi fauna is similar to that from the Apak Member at Lothagam, in particular by the domination of *Sindacharax mutetii*.

INTRODUCTION

The presence of fossil fishes at Kanapoi had been reported by Behrensmeyer (1976) among others, but no systematic recovery was initiated until 1993. Over 2,800 fossil fish elements were recovered from Kanapoi deposits in the 1993 and 1995 field seasons (see map in Introduction, page 2). Most collecting was undertaken by the author and Sam N. Muteti, of the National Museums of Kenya, with some additional collecting by the National Museums of Kenya fossil team. As discussed by Feibel (2003b), the major phase of deposition of the Kanapoi deposits date from 4.17 Ma to about 4.07 Ma with three sedimentary intervals: a lower fluvial sequence, a lacustrine phase, and an upper fluvial sequence. The fish fossils were collected from six sites located in the lacustrine phase of the formation, and from one site probably deposited during the upper fluvial sequence and hence slightly younger than 4.07 Ma.

Fieldwork at Kanapoi followed three years of intensive collection of vertebrate and invertebrate fossils from the nearby site of Lothagam (Leakey et al., 1976; Leakey and Harris, 2003), with fossiliferous deposits ranging in age from late Miocene to Holocene, as well as from the western Turkana Basin Pliocene sites of Ekora, South Turkwel, North Napudet and Eshoa Kakurongori. Reference will be made in this report to the detailed description of over 7000 fish fossils collected at the nearby site of Lothagam (Stewart, 2003). Collection of fish fossils at Lothagam was extensive, in order to obtain information on systematics, environment and biogeography, previously poorly known from this period. Most fish elements collected from Lothagam

derived from the Lower and Upper Nawata Members of the Nawata Formation, and the Apak Member of the Nachukui Formation, ranging in age from 7.44 Ma to about 4.2 Ma (McDougall and Feibel, 1999). Fish bones were also collected from the Muruogori Member, and the Kaiyumung Member of the Nachukui Formation, which date to about 4.0 Ma, and approximately 4.0 to 2.0 Ma respectively (C. Feibel, F. Brown, personal communication). More detailed information about the stratigraphy and geochronology at Lothagam is provided by Feibel (2003a) and McDougall and Feibel (1999).

Fish collecting at Kanapoi was less extensive than at Lothagam, as only elements with potential taxonomic and systematic information were collected. The Kanapoi fish elements derive from sediments which date close to 4.07 Ma, and, like the Muruogori Member sediments at Lothagam, were probably deposited during the Lonyumun Lake transgression (Feibel, 2003b). Reference will also be made to the fish collected from the Ekora site, located about 50 km southeast of Lothagam and about 25 km north of Kanapoi, near the modern Kerio River. The Ekora fauna is of Pliocene age and probably also derives from Lonyumun Lake deposits (Feibel, personal communication).

In the descriptions and discussions below, ecological and zoogeographical information on modern fish was referenced from the *Checklist of the Freshwater Fishes of Africa* volumes (Daget et al., 1984, 1986) and from Hopson and Hopson (1982).

The Kanapoi fishes have not yet been accessioned into the collections of the National Museums of Kenya. In the systematic description, the specimens are listed by the field number for their site of origin.

1. Canadian Museum of Nature, PO Box 3443, Station D, Ottawa, Ontario K1P 6P4, Canada.

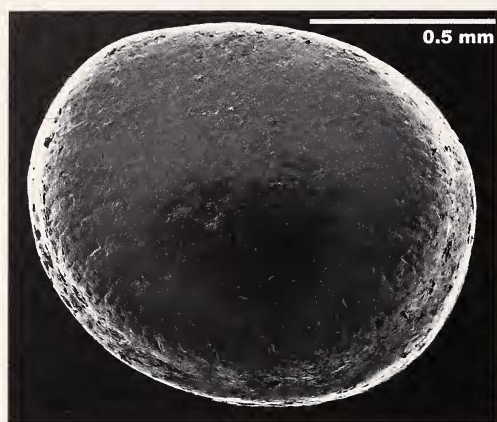


Figure 1 *Hyperopisus* sp., SEM of isolated tooth, ventral view, from Kanapoi

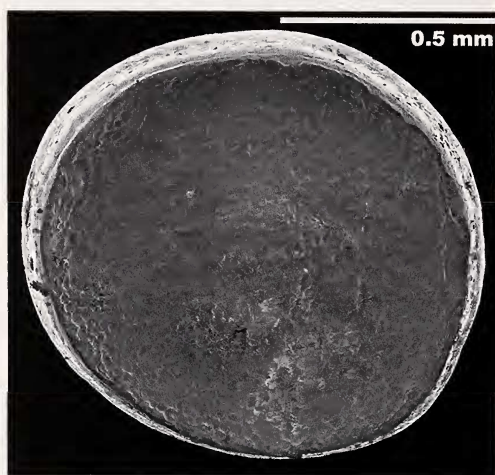


Figure 2 *Hyperopisus* sp., SEM of isolated tooth and base, dorsal view, from Kanapoi

SYSTEMATIC DESCRIPTION

Order Polypteriformes

Family Polypteridae

Polypterus Geoffroy Saint-Hilaire, 1802

Polypterus sp.

KANAPOI MATERIAL. 3156, scale.

Polypterus material is extremely rare in Kanapoi deposits, with only one element identified. As *Polypterus* scales, spines, and cranial fragments are robust and preserve well, this poor record suggests a minimal Pliocene presence at Kanapoi.

The family Polypteridae is today represented by two genera: *Polypterus* and *Calamoichthys* Smith, 1866 (rather than *Erpetoichthys* Smith, 1865; see discussion in Stewart, 2001), both restricted to Africa. Most fossil elements comprise scales, vertebrae, and spines, and have been referred to the larger and today much more widely distributed genus *Polypterus* or only to the family Polypteridae.

Polypterus is a long, slender fish with a distinctive, long dorsal fin that is divided by spines into portions resembling sails; they have a lung-like organ to breathe air. Polypteridae have several primitive features with similarities to Paleozoic paleoniscoids (Carroll, 1988). Their earliest fossil record from Africa is from Upper Cretaceous deposits in Egypt, Morocco, Niger, and Sudan (Strömer, 1916; Dutheil, 1999). Their Cenozoic record includes fossils from Eocene deposits in Libya (Lavocat, 1955); Miocene deposits in Rusinga, Loperot, and Lothagam, Kenya (Greenwood, 1951; Van Couvering, 1977; Stewart, 2003), and Bled ed Douarah, Tunisia (Greenwood, 1973); Pliocene deposits at Wadi Natrun, Egypt (Greenwood, 1972); Pliocene deposits at Lothagam, Kenya (Stewart, 2003); and Plio-Pleistocene deposits at Koobi Fora (Schwartz, 1983). *Polypterus* has never been recovered from the Western Rift sites. Two extant species are

known from Lake Turkana—*P. senegalus* Cuvier, 1829, and *P. bichir* Geoffroy Saint Hilaire, 1802. *Polypterus* is widespread from Senegal to the Nile Basin up to Lake Albert, as well as the Congo Basin and Lake Tanganyika.

Order Mormyriiformes

Family Mormyridae

Hyperopisus Gill, 1862

Hyperopisus sp.

Figures 1, 2

KANAPOI MATERIAL. 3156, 1 tooth; 3845, 96 teeth; 3847, 7 teeth; 3848, 3 teeth; 3849, 2 teeth.

Hyperopisus teeth appear as truncated cylinders with smooth, relatively flat tops and bases (Figs. 1, 2), and attach to the parasphenoid and basihyal bones. The average diameter of the Kanapoi teeth (1–4 mm) is within the range of large extant *Hyperopisus* individuals (up to 90 cm total length).

Hyperopisus teeth are relatively common throughout the Kanapoi deposits. While absent from the Nawata Formation deposits at Lothagam, the teeth are common in the Nachukui Formation deposits and at the Pliocene South Turkwell site (personal observation). Modern *Hyperopisus* (and other mormyroids) generate weak electromagnetic fields in order to sense their environment. They are therefore absent from modern Lake Turkana and other bodies of water with high salinity values, which apparently impede this sensory ability (Beadle, 1981).

Fossil *Hyperopisus* teeth (see summary in Stewart, 2001) are known from Pliocene deposits of Wadi Natrun, Egypt (Greenwood, 1972), from Plio-Pleistocene deposits in the Lakes Albert and Edward Basins (Greenwood and Howes, 1975;

Stewart, 1990), Mio–Pleistocene Lakes Albert and Edward Basins deposits (Van Neer, 1994), from Pliocene deposits at Lothagam (Stewart, 2003) and from Plio–Pleistocene deposits at Koobi Fora (Schwartz, 1983). Modern *H. bebe* Lacépède, 1803, is known from the Omo River Delta of Lake Turkana, and from the Senegal, Volta, Niger, Chad, and Nile Basins.

Large teeth referred to ?*Hyperopisus* have been reported in Pliocene Lake Edward Basin deposits and Pliocene Wadi Natrun deposits (Greenwood, 1972; Stewart, 1990, 2001). These teeth, although identical to those of modern *Hyperopisus*, far exceed the size range of modern teeth, and as no identified bone has been recovered with the teeth, their affiliation is problematic. These were not recovered in the Turkana Basin deposits, and to date have a restricted Nile River and Western Rift presence.

Family Gymnarchidae

Gymnarchus Cuvier, 1829

Gymnarchus sp.

KANAPOI MATERIAL. 3156, 18 teeth; 3845, 3 teeth; 3847, 3 teeth; 3848, 3 teeth; 3849, 7 teeth.

Gymnarchus teeth line the premaxilla and dentary. They are common throughout the Kanapoi deposits. The Kanapoi teeth average 3–4 mm in width, which is within the size range of large modern individuals (60–100 cm total length).

Gymnarchus is piscivorous, although mollusks and insects are also eaten. As in *Hyperopisus*, these fish use an electromagnetic field to sense the environment and are therefore intolerant of highly saline waters. *Gymnarchus* teeth are common throughout the Kanapoi deposits, as they are throughout the Lothagam deposits. Fossil elements are reported from Miocene–Pleistocene deposits in Lakes Albert and Edward Basins (Van Neer, 1994), Pliocene deposits in the Lakes Albert and Edward Basins (Stewart, 1990; Van Neer, 1992), late Miocene and Pliocene deposits at Lothagam, Kenya (Stewart, 2003), and Plio–Pleistocene deposits at Koobi Fora (Schwartz, 1983). Modern *G. niloticus* Cuvier, 1829, is known from the Omo River Delta in Lake Turkana, and in the Gambia, Senegal, Niger, Volta, Chad, and Nile Basins.

Order Cypriniformes

Family Cyprinidae

Labeo Cuvier, 1817

Labeo sp.

(Figures 3, 4)

KANAPOI MATERIAL. 3156, 12 teeth; 3845, 24 teeth; 3846, 4 teeth; 3847, 37 teeth; 3848, 6 teeth; 3849, 26 teeth, 1 trunk vertebra.

Labeo is essentially represented by its pharyngeal teeth, which were not identifiable to species (Figs. 3, 4). One vertebra was also recovered, and while

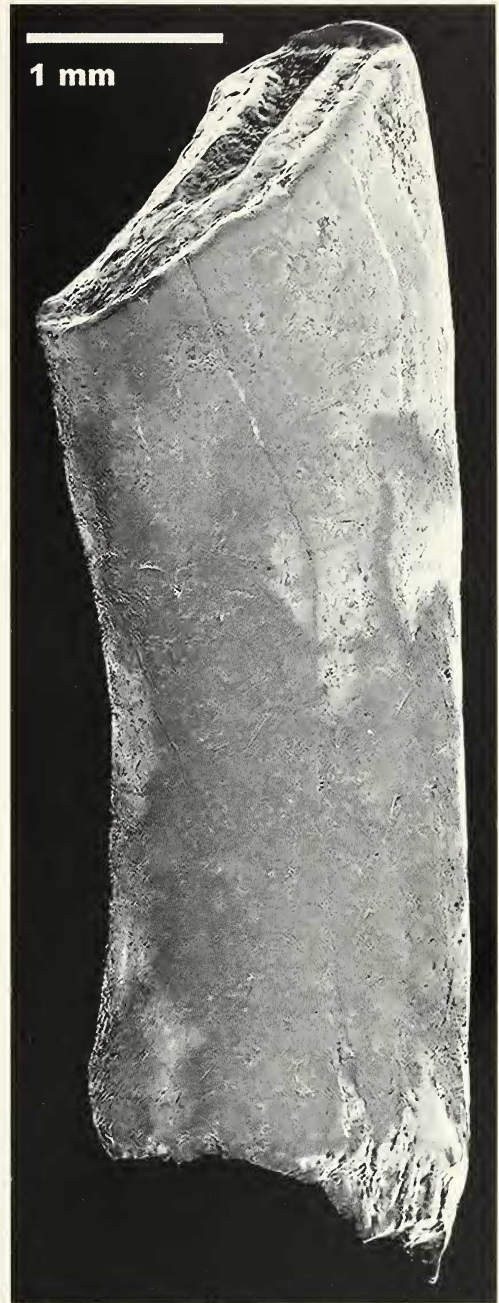


Figure 3 *Labeo* sp., SEM of pharyngeal tooth, side view, from Kanapoi

similar to *Barbus* Cuvier and Cloquet, 1816, vertebrae, *Labeo* vertebrae can be distinguished by trabecular morphology. These elements represent individuals up to 90 cm in total length, which is within the modern size range of the Turkana species.

Labeo teeth are surprisingly common throughout the Kanapoi deposits. Its teeth are rare in the Nawata Formation sites at Lothagam, but more com-



Figure 4 *Labeo* sp., SEM of pharyngeal tooth, ventral view, from Kanapoi

mon in the Nachukui Formation sites. *Labeo* is an inshore bottom fish, eating algae and organic detritus. The fossil record is scanty (Stewart, 2001), but reported from late Miocene deposits at Lothagam, Kenya (Stewart, 2003); Pliocene deposits in

Wadi Natrun, Egypt (Greenwood, 1972), Koobi Fora, Kenya (Schwartz, 1983), the Lakes Albert and Edward Basins (Stewart, 1990); and Pleistocene deposits in the Western Rift (Van Neer, 1994). A reported Miocene occurrence from western Uganda may be in error; the author states that certain Mio-Pliocene sites had Pleistocene-aged fossils mixed in (Van Neer, 1994:90). *Labeo*-like teeth are also reported from the mid-Miocene of Loperot but are not confirmed (Van Couvering, 1977). In Lake Turkana, extant *Labeo* is represented by one species—*L. horie* Heckel, 1846. Elsewhere, the genus is widespread throughout the continent, including the Nile Basin, West Africa, eastern Africa, and the Congo and Zambezi Basins.

Barbus Cuvier and Cloquet, 1816

Barbus sp.

(Figures 5, 6)

KANAPOI MATERIAL. 3156, 4 teeth; 3845, 2 teeth; 3846, 3 teeth; 3849, 6 teeth.

Barbus is exclusively represented by its pharyngeal teeth (Figs. 5, 6), which represent small individuals, probably under 30 cm total length. These teeth do not resemble those of *B. bynni* Boulenger, 1911, the only similar sized *Barbus* now inhabiting Lake Turkana, but do resemble those of *B. altianalis* Boulenger, 1900; no other comparison with modern *Barbus* species was made. The teeth do not have the rows of small cusps observed on some *Barbus*? teeth recovered from Miocene deposits in Saudi Arabia (Otero and Gayet, 2001).

Like *Labeo*, *Barbus* is an inshore demersal (bottom-dwelling) fish, with a varied diet of ostracods, mollusks, insects, aquatic vegetation, and occasionally fishes. *Barbus* teeth are not common at Kanapoi, nor are they common at nearby Lothagam

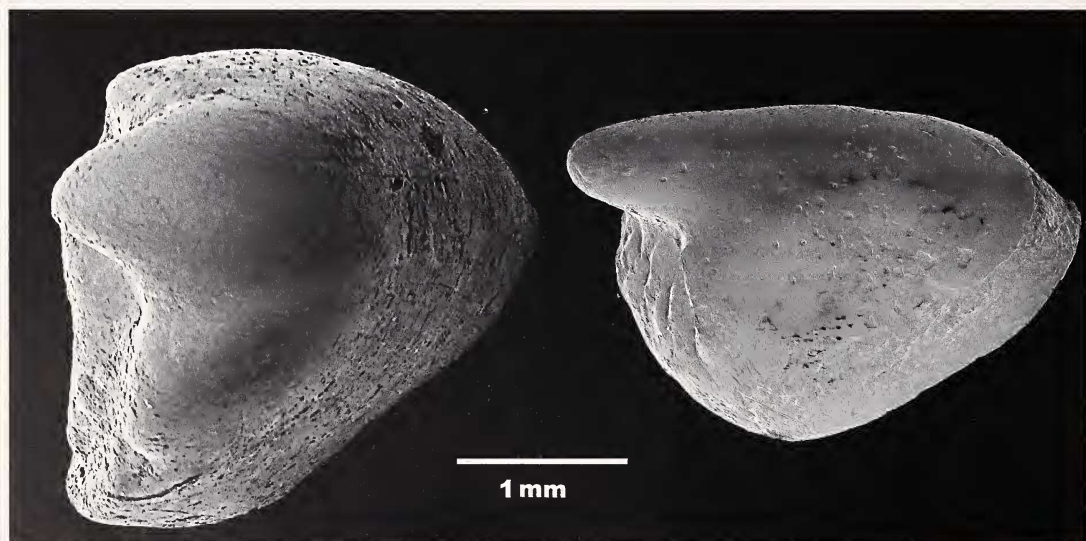


Figure 5 *Barbus* sp., SEM of pharyngeal tooth, ventral view (left) and side view (right), from Kanapoi

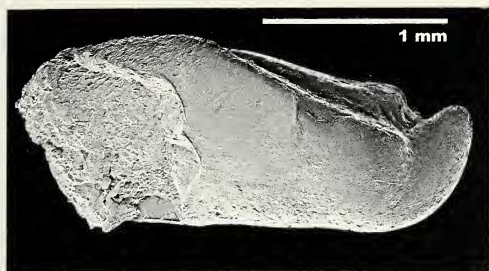


Figure 6 *Barbus* sp., SEM of pharyngeal tooth (different from Fig. 5), side view, from Kanapoi

(Stewart, 2003). Their fossil record in Africa is virtually nonexistent prior to the Pliocene (Stewart, 2001), with the earliest reported finds being from Pliocene deposits at Lothagam (Stewart, 2003), Pliocene deposits in the Western Rift, Congo (Stewart, 1990), Plio-Pleistocene deposits from Koobi Fora (Schwartz, 1983), and Pleistocene deposits from the Western Rift (Greenwood, 1959; Van Neer, 1994). Van Couvering (1977) notes that “*Barbus*-like” teeth are known from mid-Miocene deposits in Kenya. The report of a probable *Barbus* in Miocene deposits in Saudi Arabia (Otero, 2001; Otero and Gayet, 2001) indicates these fishes could have entered Africa from the Arabian region during land connections in the Burdigalian (early Miocene) (see discussion in Otero, 2001).

At present, *Barbus* is represented by three species in Lake Turkana, with only *B. bynni* attaining a length of at least 30 cm in Lake Turkana.

Order Characiformes

Family Distichodontidae

Distichodus Müller and Troschel, 1845

Distichodus sp.

(Figure 7)

KANAPOI MATERIAL. 3156, 1 tooth; 3845, 2 teeth; 3847, 2 teeth; 3849, 3 teeth.

Distichodus teeth are oral, lining the premaxilla and dentary (Fig. 7). The average height of the Kanapoi teeth was 5 mm long, which is within the size range of modern individuals.

Distichodus remains are not common at Kanapoi nor at Lothagam, but this may reflect their small size and probable poor preservation. The fossil record is poor (Stewart, 2001) but is known from Mio-Pliocene deposits in the Lakes Albert and Edward Basins (Van Neer, 1994), Pliocene deposits in the Lakes Albert and Edward Basins (Stewart, 1990), late Miocene deposits at Lothagam, Kenya (Stewart, 2003), and Pleistocene deposits at Koobi Fora (Schwartz, 1983). Extant *D. niloticus* (Linnaeus, 1762) is known from Lake Turkana and from the Nile Basin up to Lake Albert.



Figure 7 *Distichodus* sp., SEM of oral tooth, side view, from Kanapoi

Family Alestidae

Hydrocynus Cuvier, 1817

Hydrocynus sp.

(Figure 8)

KANAPOI MATERIAL. 3156, 23 teeth, 1 dentary fragment with tooth; 3845, 33 teeth, 1 dentary fragment with tooth; 3846, 3 teeth; 3847, 13 teeth, 1 dentary fragment with tooth, 1 premaxilla fragment; 3848, 32 teeth, 4 dentary fragments, 4 dentary fragments with teeth, 1 premaxilla fragment; 3849, 2 teeth.

Hydrocynus teeth are long and conical in shape (Fig. 8), with considerable size range. At Kanapoi, both teeth and jaw elements were recovered, often with the teeth in situ, usually in replacement sockets within the jaw element. Teeth and jaw elements



Figure 8 *Hydrocynus* sp., SEM of oral tooth and base, side view, from Kanapoi

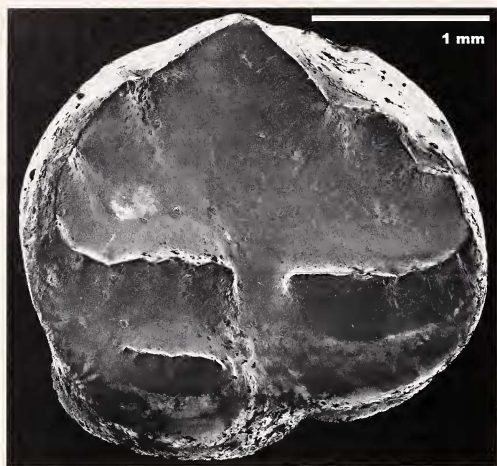


Figure 9 *Brycinus macrolepidotus*, SEM of second inner premaxillary tooth, occlusal view, from Kanapoi; labial side at bottom, lingual at top

represent individuals of up to 1 m in total length, although modern individuals in Lake Turkana do not exceed 65 cm in total length (Hopson and Hopson, 1982). Several small teeth with a broader base and more triangular shape than most teeth were determined, from modern *Hydrocynus* jaws, to be teeth which were just erupting.

The fossil record of *Hydrocynus* has been primarily based on teeth (Stewart, 2001); therefore, the recovery of jaw elements potentially provides new information about the fossil genus. *Hydrocynus* are pelagic and are voracious piscivores. Fossil *Hydrocynus* teeth are known from Mio-Pleistocene deposits in the Western Rift, Uganda (Van Neer, 1994), Miocene deposits of Sinda, Congo (Van Neer, 1992), late Mio-Pliocene deposits at Lothagam, Kenya (Stewart, 2003), Pliocene deposits in Wadi Natrun, Egypt (Greenwood, 1972), and the Western Rift, Congo (Stewart, 1990), and Plio-Pleistocene deposits in the Omo Valley (Arambourg, 1947) and at Koobi Fora (Schwartz, 1983). *Hydrocynus* is represented by one species, *H. forskalii* Cuvier, 1819, in Lake Turkana, but a second species, *H. vittatus* Castelnau, 1861, is present in the Omo River. *Hydrocynus* is widespread from Senegal to the Nile, including the Volta, Niger, and Chad Basins.

Brycinus Myers, 1929

B. macrolepidotus
(Cuvier and Valenciennes, 1849)
(Figures 9–11)

KANAPOI MATERIAL. 3156, 1 second inner premaxillary tooth.

Brycinus is represented only by a second inner premaxillary tooth (Fig. 9) which is identical to the

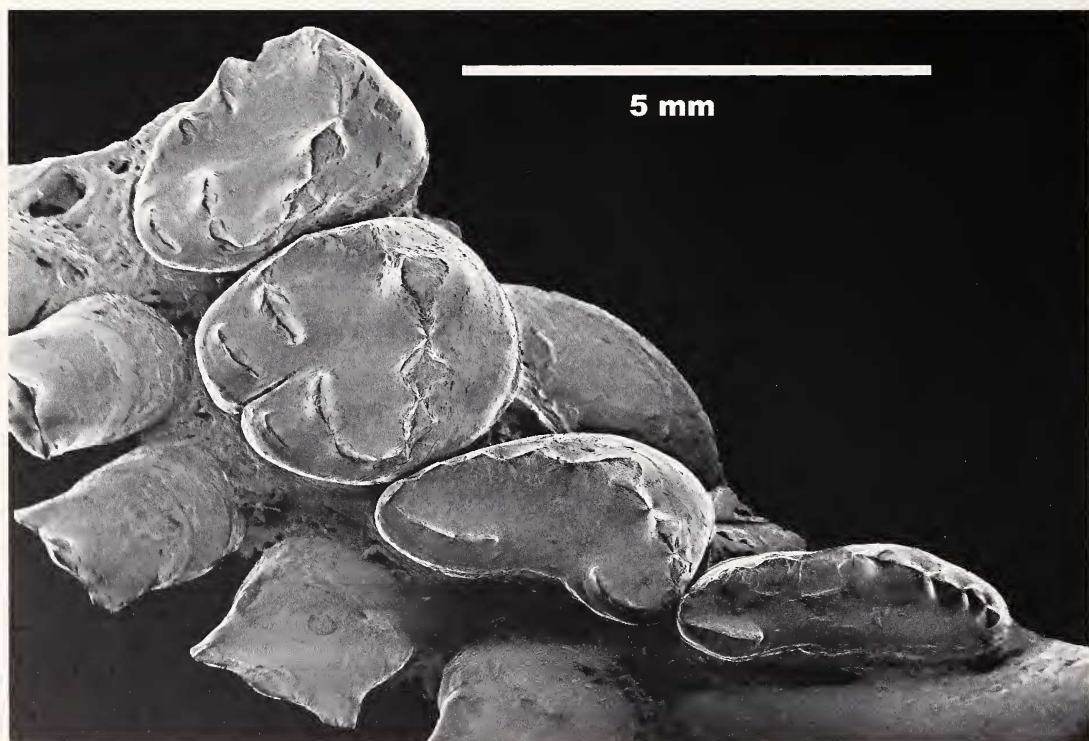


Figure 10 *Brycinus macrolepidotus*, SEM of first, second, third, and fourth inner premaxillary teeth (from left to right) and some outer teeth, occlusal views; lingual side at top right, labial at bottom left; modern specimen

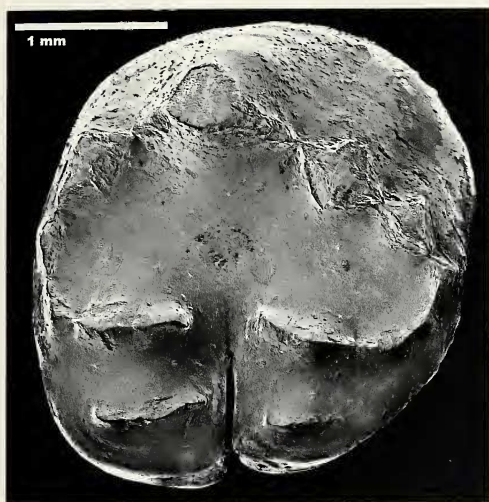


Figure 11 *Brycinus macrolepidotus*, SEM of second inner premaxillary tooth, occlusal view; labial side at bottom, lingual at top; modern specimen

same tooth in modern *B. macrolepidotus* specimens (Figs. 10, 11). *Brycinus macrolepidotus* has distinctive inner premaxillary teeth, which are not found in other alestid specimens. The tooth represents an individual of about 30 cm in total length.

A recent study has transferred *Alestes macrolepidotus* and twelve other *Alestes* Muller and Troschel 1844 species to the genus *Brycinus*, leaving five species in the genus *Alestes*, and five in a polyphyletic grouping referred to as “*Brycinus*” (Murray and Stewart, 2002). Both *Alestes* and *Brycinus* are genera within the Alestidae, which possess similar multicusped molariform teeth. In the following discussions, I will use “alestid” to refer to *Alestes* and/or *Brycinus*, but not to *Hydrocynus*, which is also alestid but with very different, conical teeth (see Murray and Stewart, 2002, for discussion of the terms Alestidae, “Hydrocyninae,” and “Alestinae”).

Use of fine-meshed screens at several sites resulted in recovery of many small cusped teeth, which in the field were thought to belong to *Alestes* or *Brycinus*. Closer inspection with a microscope revealed that these teeth actually belonged to *Sindacharax*, based on similarity to larger specimens (see discussion under *Sindacharax* Greenwood and Howes, 1975). The recovery of only one *Brycinus* tooth, particularly when fine-meshed screens (1-mm mesh) were used at several sites indicates the scarcity of this taxon at Kanapoi. *Brycinus* and *Alestes* were slightly more common at Lothagam.

The fossil record of *Brycinus* sp. (and *Alestes* sp.) is poor (Stewart, 2001), with remains known from Mio-Pliocene deposits at Lothagam, Kenya (Stewart, 2003), Plio-Pleistocene deposits in the Lakes Albert and Edward Basins (Stewart, 1990), Mio-Pleistocene deposits in the Western Rift (Van Neer,

1994), and Manonga, Tanzania (Stewart, 1997). Miocene teeth with alestid affinities are reported from Loperot and Mpesida, Kenya (Van Couvering, 1977). Modern alestids are represented by six species in Lake Turkana, including *A. baremoze* de Joannis, 1835; *A. dentex* Linnaeus, 1758; *B. nurse* Rüppell, 1832; *B. macrolepidotus*; *B. ferox* Hopson and Hopson, 1982; and *B. minutus* Hopson and Hopson, 1982. Modern alestids are found in the Volta, Niger, and Chad Basins to the Nile River, and in the Congo, Zambezi, and Limpopo Basins. Modern alestid species span a range of trophic adaptations and habitats. In modern Lake Turkana, they are generally pelagic and omnivorous.

Sindacharax Greenwood and Howes, 1975

A total of 2,272 teeth from Kanapoi are attributed to *Sindacharax*. This preponderance of *Sindacharax* teeth compared to numbers of elements of other fish reported here does not reflect actual abundance, but a selective collection policy.

Very few *Sindacharax* dentaries and/or premaxillae are known with in situ teeth, and none from Kanapoi, so identification of isolated teeth was accomplished by comparison with the complete dentary and premaxilla of *S. greenwoodi* Stewart, 1997, found at Lothagam (Stewart, 1997). However, because there is considerable individual variation in cusp patterns of teeth in known *Sindacharax* jaws, placement of these isolated teeth is tentative. Analysis of the in situ teeth and the isolated teeth at Lothagam indicated that outer premaxillary and dentary teeth were so similar among *Sindacharax* species, as were third and fourth inner premaxillary teeth, that no species designations for these teeth are made. As is the common convention, in this article, teeth are numbered sequentially, starting from the midline of the jaw (#1 left or right) and moving laterally.

As mentioned above in the discussion on modern alestids, many very small teeth (<2 mm) were recovered, which were initially thought to belong to *Brycinus* or *Alestes*, until closer examination indicated they were very small *S. mutetii* Stewart, 2003, and *S. lothagamensis* Stewart, 2003, teeth. The similarity in shape and cusping between small *Sindacharax* and modern alestid teeth leads to speculation on the development of the characteristic cusped ridges in *Sindacharax* teeth for which the genus is named (Greenwood and Howes, 1975; Greenwood, 1976). Examination of a range of *Sindacharax* inner premaxillary teeth indicates that, while the smaller teeth (ca. <2 mm) are cusped, in larger teeth, the cusps morph to form ridges. Once the ridges are formed, the tooth pattern remains consistent.

On the other hand, in several of the modern alestid specimens observed by the author (including *B. macrolepidotus*, *A. dentex*, *A. baremoze*), the inner teeth remained cusped in both large and small specimens, with one exception. Small *A. stuhlmanni*



Figure 12 *Sindacharax lothagamensis*, SEM of second inner premaxillary tooth, occlusal view, from Kanapoi; labial side at top, lingual at bottom

Pfeffer, 1896, individuals had cusped teeth, but the larger specimens (ca. 24 cm in total length) had teeth with ridges (personal observation). Of particular interest therefore is whether teeth of other modern alestid species develop ridges after achieving a certain length and whether these teeth can be distinguished from *Sindacharax* teeth. This leads to some taxonomic difficulties, as the genus *Sindacharax* was erected based on its supposedly unique ridged teeth. While the analysis of existing *Sindacharax* jaw elements demonstrates enough differences with modern alestid elements to keep *Sindacharax* as a separate genus, the diagnosis of the *Sindacharax* genus needs to be re-examined in order to define it more accurately. However, more *Sindacharax* cranial and postcranial elements must be recovered for such revision.

Sindacharax lothagamensis Stewart, 2003
(Figures 12, 13)

KANAPOI MATERIAL. 3156, 2 second inner premaxillary teeth; 3848, 1 first inner premaxillary tooth; 3849, 17 first inner premaxillary teeth, 57 second inner premaxillary teeth; 29287, 7 first inner premaxillary teeth.

Teeth of *Sindacharax lothagamensis* are smaller on average than those of other *Sindacharax* and are relatively common at Kanapoi. The Kanapoi second inner premaxillary teeth are identical to both the holotype and the isolated teeth found at Lothagam (e.g., Stewart, 2003: fig. 3.5) (Fig. 12). The size range of teeth differs slightly from that at Lothagam; at Lothagam, second inner premaxillary teeth ranged up to 5.5 mm in length with most under 3 mm, whereas the Kanapoi teeth ranged to 5 mm, with most under 2 mm. Numerous first inner teeth were found associated with the second inner



Figure 13 *Sindacharax lothagamensis*, SEM of first inner premaxillary tooth, occlusal view, from Kanapoi; labial side at top, lingual at bottom

teeth at Kanapoi, particularly at site 3849, and they showed a slightly different cusp pattern than that described for the Lothagam teeth (Stewart, 2003). These Kanapoi first teeth are long and narrow, with the dominant cusp at the lingual end of the tooth. A smaller cusp, not two, veers in a diagonal line towards the presumed bucco-labial side, and another cusp is positioned anterior to the dominant cusp. Anterior to this are one or more ridges traversing the width of the tooth (Fig. 13).

Sindacharax lothagamensis teeth were the second most numerous of *Sindacharax* teeth at Kanapoi. This abundance of *S. lothagamensis* is a surprise, as they were primarily recovered in the late Miocene Lower Nawata deposits at Lothagam and only occasionally in later Pliocene deposits. Their abundance at Kanapoi suggests that absence in later Lothagam deposits may reflect a collection bias or different environmental conditions. Collection bias seems unlikely, as intensive collecting occurred at Pliocene deposits in Lothagam. However, different environmental conditions from the late Miocene to Pliocene deposits at Lothagam is certainly possible, with the latter providing unfavorable habitats for



Figure 14 *Sindacharax mutetii*, SEM of first inner premaxillary tooth, occlusal view, from Kanapoi; labial side at top, lingual at bottom

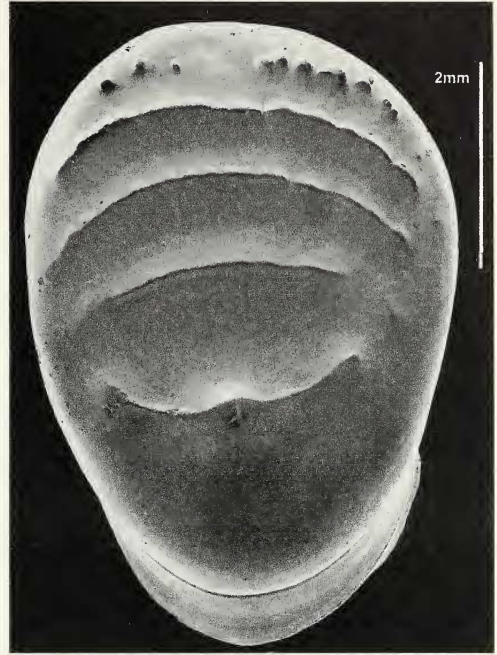


Figure 15 *Sindacharax mutetii*, SEM of second inner premaxillary tooth, occlusal view, from Kanapoi; labial side at top, lingual at bottom

S. lothagamensis, and Kanapoi may have provided a more favourable environment for them.

Sindacharax mutetii Stewart, 2003
(Figures 14–17)

EMENDED DIAGNOSIS. Second inner premaxillary tooth distinguished from *Sindacharax lepersonnei* Greenwood and Howes, 1975 and *S. lothagamensis* by cusps forming ridges rather than discrete cusps as in *S. lepersonnei* and *S. lothagamensis*. Distinguished from *S. deserti* Greenwood and Howes, 1975, by absence of raised circular ridge radiating from the dominant lingual cusp; distinguished from *S. greenwoodi* Stewart, 1997, by lack of the ridged arc surrounding dominant lingual cusp, and distinguished from all other *Sindacharax* by broad oval shape.

HOLOTYPE. A second inner premaxillary tooth, collected from Lothagam by Sam N. Muteti and Peter Kiptalam in 1993 from Site 1944 in the Apak Member of the Nachukui Formation, and now housed in the collections of the National Museums of Kenya, Nairobi, with the accession number KNM-LT 38265.

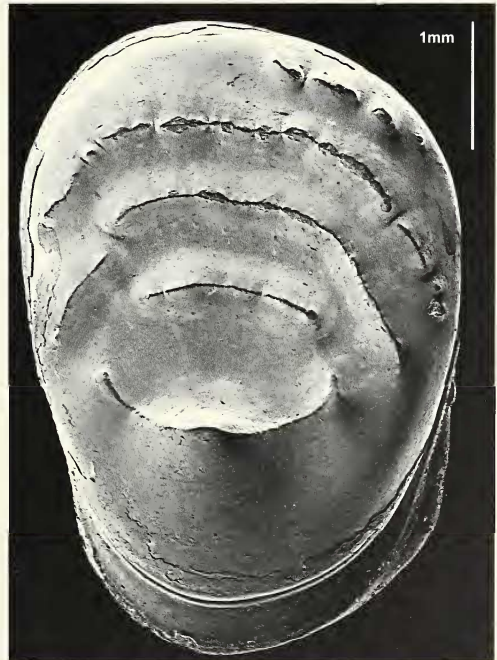


Figure 16 *Sindacharax mutetii*, SEM of second inner premaxillary tooth, occlusal view, from Kanapoi; labial side at top, lingual at bottom



Figure 17 *Sindacharax mutetii*, SEM of in situ second and third inner premaxillary teeth, occlusal view, from Kanapoi; labial side at top, lingual at bottom, medial to the right, lateral to the left

KANAPOI MATERIAL. 3156, 3 second inner premaxillary teeth; 3845, 21 first inner premaxillary teeth, 26 second inner premaxillary teeth; 3846, 14 first inner premaxillary teeth, 39 second inner premaxillary teeth; 3847, 51 first inner premaxillary teeth, 75 second inner premaxillary teeth; 3848, 43 first inner premaxillary teeth, 67 second inner premaxillary teeth; 3849, 50 first inner premaxillary teeth, 73 second inner premaxillary teeth; ngui site, 28 first inner premaxillary teeth, 65 second inner premaxillary teeth.

Most first and second inner premaxillary teeth recovered were identical to those recovered from the Apak and Kaiyumung Members at Lothagam (Stewart, 2003) (Figs. 14, 15); however, a few second inner premaxillary teeth showed a slight deviation in cusp pattern (Fig. 16). Instead of the first ridge, which is anterior to the dominant cusp, traversing the whole width of the tooth, in some teeth it was shortened and often bracketed by one or both ends of the ridge anterior to it.

The large number of *S. mutetii* teeth recovered at Kanapoi reflect a range of individual variations in their cusp patterns. Several of the second and third inner premaxillary teeth recovered have similar patterns to their counterparts in situ on the premaxilla recovered from the Apak Member at Lothagam, which was ascribed to cf. *S. mutetii* (Stewart, 2003). Therefore, the Lothagam premaxilla is now included in *S. mutetii* (Fig. 17). This premaxilla re-

mains the only jaw element recovered which is ascribed to *S. mutetii*.

A total of 555 teeth ascribed to *S. mutetii* were recovered at Kanapoi, making it the most abundant of the *Sindacharax* species at that site. *Sindacharax mutetii* teeth were also the most common teeth recovered from the Apak Member deposits at Lothagam, although this species was not recovered from the Murongori Member.

Stewart (2003) stated that *S. mutetii* was the only *Sindacharax* found at Kanapoi. However, further study of the Kanapoi specimens showed that, while *S. mutetii* is by far the most common species recovered, teeth of both *S. lothagamensis* and *S. howesi* Stewart, 2003, are also present.

Sindacharax howesi Stewart, 2003

KANAPOI MATERIAL. 3845, 3 first inner premaxillary teeth; 3846, 1 first inner premaxillary tooth; 3847, 8 first inner premaxillary teeth; 3848, 7 first inner premaxillary teeth, 2 second inner premaxillary teeth; 29287, 1 second inner premaxillary tooth.

Sindacharax howesi teeth were not common at Kanapoi. Mainly first inner premaxillary teeth were recovered, and these were identical to those found in the northern Kaiyumung deposits at Lothagam.

Sindacharax howesi teeth were exclusively found in the north Kaiyumung deposits at Lothagam, where they are numerous. Their appearance in the



Figure 18 *Sindacharax* sp., SEM of in situ third inner premaxillary tooth, from Kanapoi; labial side at top, lingual at bottom

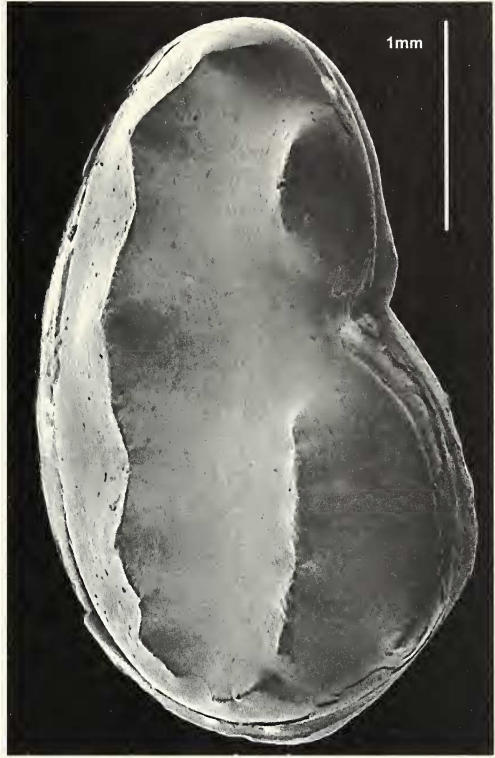


Figure 19 *Sindacharax* sp., SEM of in situ fourth inner premaxillary tooth, from Kanapoi; labial side probably to the right, lingual probably to the left

Kanapoi deposits indicates a slightly earlier presence (ca. 4.0 Ma) in the Turkana Basin than previously thought.

Sindacharax sp.
(Figures 18, 19)

As discussed above, outer premaxillary and dentary teeth are indistinguishable between the species, and therefore are referred as *Sindacharax* sp. Similarly, third and fourth inner premaxillary teeth are similar among the species, and again were referred to *Sindacharax* sp.

Third and Fourth Inner Premaxillary Teeth

KANAPOI MATERIAL. 3845, 16 third or fourth inner premaxillary teeth; 3846, 11 third or fourth inner premaxillary teeth; 3847, 43 third inner premaxillary teeth, 15 fourth inner premaxillary teeth; 3848, 25 third or fourth inner premaxillary teeth; 3849, 32 third or fourth inner premaxillary teeth; 29287, 12 third or fourth inner premaxillary teeth.

No third or fourth inner premaxillary teeth could be assigned to species, as they were very similar throughout the deposits. Often the third and fourth teeth could not be distinguished from each other, as the only confirmed fourth premaxillary tooth (preserved in situ on the *S. greenwoodi* type speci-

men) is very worn and the cusp pattern almost indistinguishable. However, based on comparison with the *S. greenwoodi* premaxilla and modern *Alestes* and *Brycinus* premaxillae, I have tentatively assigned some teeth as third inner teeth (Fig. 18) and fourth inner teeth (Fig. 19).

Outer Teeth

While outer teeth are difficult to distinguish between species, there are several distinct types. Similar to the Lothagam outer teeth (Stewart, 2003a), I have classified the Kanapoi teeth into types, with an indication to which species they are most consistently associated.

Outer Premaxillary Teeth, Type A

KANAPOI MATERIAL. 3156, 4 outer premaxillary teeth; 3845, 26 outer premaxillary teeth; 3846, 10 outer premaxillary teeth; 3847, 86 premaxillary outer teeth; 3848, 48 premaxillary outer teeth; 3849, 22 premaxillary outer teeth; 29287, 19 premaxillary outer teeth.

Type A teeth consist of one dominant and two much smaller flanking cusps, which slope into a short, uncusped platform on one side but have a steep shelf on the other side (see figs. 3.26 and 3.27

in Stewart, 2003). They have a round or oval attachment base. At Kanapoi, Type A teeth are associated with both *S. lothagamensis* and *S. mutetii* teeth; when associated with *S. mutetii*, they often have elongated attachment bases.

Outer Premaxillary Teeth, Type B

KANAPOI MATERIAL. 3845, 5 outer premaxillary teeth; 3846, 2 outer premaxillary teeth; 3847, 11 outer premaxillary teeth; 3848, 11 outer premaxillary teeth; 3849, 3 outer premaxillary teeth; 29287, 1 outer premaxillary tooth.

Type B teeth are similar to Type A but have one or more discrete cusps at the base of the platform (Stewart, 2003: figs. 3.26, 3.27). Their attachment base is round or a roundish oval. These teeth were most common in sites where *S. howesi* was also found.

Outer Premaxillary Teeth, Type C

KANAPOI MATERIAL. 3848, 5 outer premaxillary teeth.

Type C teeth have a dominant central cusp, flanked by concentric or semiconcentric rows of small cusps (Stewart, 1997: figs. 2, 3). Their attachment base is an elongated oval. These teeth were rare at Kanapoi, and no particular affiliation can be ascertained.

Outer Dentary Teeth

The outer dentary teeth recovered were mainly first, second, and third teeth; fourth teeth are much smaller and fewer have been recovered. The first tooth is usually truncated posteriorly, to accommodate the inner tooth. There is considerable wear visible on most dentary teeth, and it is often difficult to describe any morphology on the teeth. As with premaxillary outer teeth, outer dentary teeth can be divided into types, although only Type A was recovered at Kanapoi.

Outer Dentary Teeth, Type A

KANAPOI MATERIAL. 3156, 5 outer dentary teeth; 3845, 85 outer dentary teeth; 3846, 61 outer dentary teeth; 3847, 205 outer dentary teeth; 3848, 134 outer dentary teeth; 3849, 295 outer dentary teeth; 29287, 122 outer dentary teeth.

All dentary teeth recovered at Kanapoi belonged to Type A, although many were too worn to ascertain type. These teeth have a dominant, pointed cusp and are flanked by two smaller cusps, which form a shelf on one side, more elongated and less steep than that of the premaxillary teeth (illustrated in Stewart, 2003). On the other side, the cusps slope into a broad platform, which is usually uncusped but may be weakly cusped. The attachment base is much more elongated than in most premaxillary teeth. Outer dentary teeth were by far the most abundant of all *Sindacharax* teeth, probably because of their size and robust attachment bases.

Inner Dentary Teeth

KANAPOI MATERIAL. 3845, 8 inner dentary teeth; 3846, 4 inner dentary teeth; 3847, 22 inner dentary teeth; 3848, 7 inner dentary teeth; 3849, 5 inner dentary teeth; 29287, 5 inner dentary teeth.

These teeth are very similar in both *Alestes* and *Sindacharax*. There is only one inner tooth on each dentary in living individuals, and it is positioned posterior to a notch in the first outer dentary tooth. Inner dentary teeth are small and round in shape, with a single elongated centrally placed cusp.

Worn and/or Fragmented Teeth, Unassigned to Position

KANAPOI MATERIAL. 3156, 1 tooth; 3845, 6 teeth; 3846, 48 teeth; 3847, 85 teeth; 3848, 50 teeth; 3849, 4 teeth; 29287, 50 teeth.

Order Siluriformes

Family Bagridae or Family Claroteidae

KANAPOI MATERIAL. 3156, 1 pectoral spine fragment; 3847, 1 cranial spine.

These catfish elements are referred to the family level both because of their incomplete nature and the similarity of these elements between some bagrid and claroteid species. They represent small individuals, probably no longer than 50 cm in total length.

Bagrid and/or claroteid catfish elements were common in the field at Kanapoi, often representing large individuals (approximately 1 m in length). Most of these elements were not collected. Many of these appeared to belong to *Clarotes* Kner, 1855, a large catfish which today often inhabits deltaic regions. Bagrids and claroteids, particularly *Bagrus* Bosc, 1816, and *Clarotes*, are known from the Mio-Pliocene deposits at Lothagam (Stewart, 2003) and at Koobi Fora (Schwartz, 1983), as well as other Cenozoic deposits in Africa. They do not appear to have radiated in the Turkana Basin as they did in the Western Rift (Stewart, 2001), although they are more common in the Plio-Pleistocene deposits at eastern Turkana.

Family Clariidae

Clarias Scopoli, 1777

Heterobranchus Geoffroy Saint-Hilaire, 1809

Clarias sp. or *Heterobranchus* sp.

KANAPOI MATERIAL. 3847, 2 caudal vertebrae; 3849, 2 trunk vertebrae, 1 caudal vertebrae.

These vertebrae are referred to *Clarias* or *Heterobranchus* because of great similarity between the elements. These vertebrae derive from small individuals (<50 cm total length).

Clariid elements were abundant at Kanapoi, but not collected. As with the bagrid catfish, many elements appeared to come from large individuals, up to 2 m in length. *Clarias* is a bottom-dwelling, in-

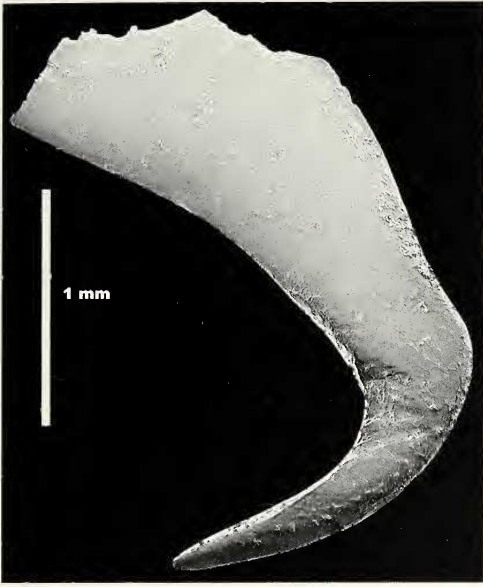


Figure 20 *Synodontis* sp., SEM of dentary tooth, from Kanapoi; side view

shore fish, which can tolerate highly deoxygenated waters. Clariid remains were common throughout the Lothagam deposits (Stewart, 2003) and in late Cenozoic deposits of Africa (Stewart, 2001). Tentative identifications are reported in the mid-Miocene from Bled ed Douarah, Tunisia (Greenwood, 1973), and Ngorora, Kenya (Schwartz, 1983). Definite clariid remains are known from Miocene deposits in Sinda, Congo (Van Neer, 1992), and Chalouf, Egypt (Priem, 1914); Mio-Pliocene deposits in Manonga, Tanzania (Stewart, 1997); Mio-Pleistocene deposits in the Western Rift (Van Neer, 1994); Pliocene deposits in Wadi Natrun, Egypt (Greenwood, 1972); and Plio-Pleistocene deposits at Koo bi Fora (Schwartz, 1983). Extant *Clarias* is represented by *C. lazera* Cuvier and Valenciennes, 1840, in Lake Turkana. *Clarias* is widespread throughout Africa, including the Nile, Congo, and Zambezi Basins.

Heterobranchus has a similar appearance and size to *Clarias*, but may be more sensitive to high salinity values. Modern *H. longifilis* Valenciennes, 1840, is present in Lake Turkana, but is rare. Like *Clarias*, *Heterobranchus* is widespread throughout the major river basins of Africa. It was identified in late Pleistocene Lake Edward Basin (Congo) deposits (Greenwood, 1959).

Family Mochokidae

Synodontis Cuvier, 1817

Synodontis sp.

(Figures 20, 21)

KANAPOI MATERIAL. 3845, 5 teeth; 3847, 1 cranial spine base.

Synodontis teeth were not common in the Kanapoi sites sampled, suggesting *Synodontis* was not a dominant presence at Kanapoi. The teeth are located on the dentary and are curved (Fig. 20). They averaged about 1 mm in width, similar to modern *Synodontis* in Lake Turkana, suggesting the fossil fish reached 30–35 cm in total length (and much larger than the other Lake Turkana mochokid, *Mochocus* de Joannis, 1935, which reaches only 6.5 cm in length). The cranial spine base recovered is fragmentary (Fig. 21) but very similar to that of modern *Synodontis*. In life, it is positioned anterior to the dorsal cranial spine and resembles a truncation of the spine.

Synodontis was probably not common at Kanapoi, as its remains normally preserve well. It was also not common at Lothagam, although consistently present through the deposits. *Synodontis* inhabits all zones of lakes and rivers, and is omnivorous, eating insects, small fish, mollusks, and zooplankton. Fossil *Synodontis* is also known from Miocene deposits at Rusinga and Chianda, Kenya (Greenwood, 1951; Van Couvering, 1977), Moghara and Chalouf, Egypt (Priem, 1920), and Bled ed Douarah, Tunisia (Greenwood, 1973); Mio-Pleistocene deposits in the Western Rift (Greenwood and Howes, 1975; Van Neer, 1992, 1994); Pliocene deposits in the Western Rift (Stewart, 1990) and Wadi Natrun (Greenwood, 1972); and Plio-Pleistocene deposits at Koo bi Fora (Schwartz, 1983). Two species of *Synodontis* inhabit modern Lake Turkana—*S. schall* Bloch and Schneider, 1801, and *S. frontosus* Vaillant, 1895. *Synodontis* is also widespread in systems throughout the African continent.

Order Perciformes

Suborder Percoidei

Family Latidae

Lates Cuvier, in

Cuvier and Valenciennes, 1828

Lates niloticus (Linnaeus, 1758)

KANAPOI MATERIAL. 3845, 1 hyomandibular, 1 premaxilla, 1 dentary, 1 first trunk vertebra, 2 trunk vertebrae, 1 caudal vertebra; 3847, 2 premaxillae, 2 posttemporal, 1 quadrate, 1 articular, 1 basioccipital fragment, 1 vomer, 6 first trunk vertebra, 1 trunk vertebra; 3848, 1 basioccipital, 1 premaxilla, 1 vomer.

These elements are identical to those in modern *Lates niloticus* and represent fish of a diverse size range. Several large fossil elements were compared with modern *L. niloticus* elements recovered from the lake margin, and these indicated that many of the Kanapoi fish had an estimated total length of over 2 m.

Many elements of *Lates niloticus* were observed in the field at Kanapoi, but only those listed above were collected, for their diagnostic value. Many of

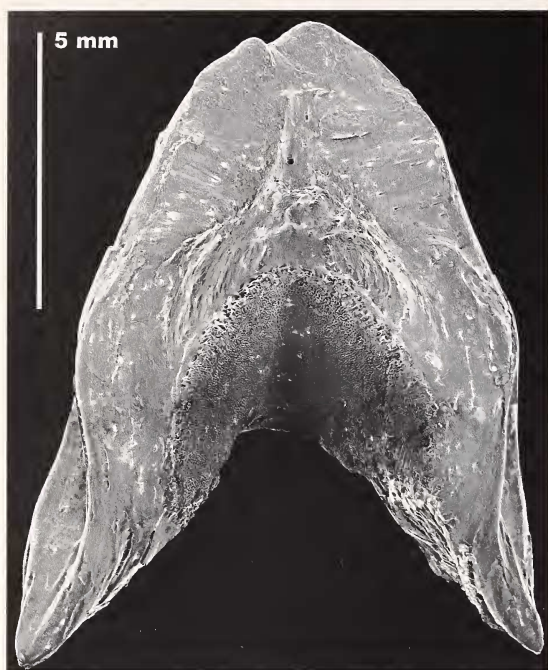


Figure 21 *Synodontis* sp., SEM of cranial spine base, from Kanapoi, ventral view

the bones represented large individuals, estimated to be approximately 2 m in length. Clearly, *L. niloticus* was a common component of the Kanapoi fish fauna, and with many large individuals must have been one of the most voracious consumers of fish in the aquatic food chain. Modern *Lates* inhabits most zones of lakes and rivers, although it only tolerates well-oxygenated waters. It is highly piscivorous.

Elements of fossil *Lates* spp. are common in African deposits (Stewart, 2001) and are known from Miocene deposits from Rusinga, Kenya (Greenwood, 1951), Gebel Zelten and Cyrenaica, Libya, (Arambourg and Magnier, 1961), Moghara and Chalouf, Egypt (Priem, 1920), Bled ed Douarah, Tunisia (Greenwood, 1973); Mio-Pliocene deposits at Lothagam, Kenya (Stewart, 2003); Plio-Pleistocene deposits from Lakes Albert and Edward Basins (together with *Semlikiichthys rhachirhynchus*) (Greenwood, 1959; Greenwood and Howes, 1975; Stewart, 1990; Van Neer, 1994); an unpublished report from Marsabit Road, Kenya (in Schwartz, 1983), the lower Omo Valley (Arambourg, 1947), and Koobi Fora (Schwartz, 1983); and Pliocene deposits from Manonga, Tanzania (Stewart, 1997), and Wadi Natrun, Egypt (Greenwood, 1972). *Lates niloticus* has also been reported from Messinian (late Miocene) deposits in Italy, the only confirmed report of this species in Europe (Otero and Sorbini, 1999). Elements formerly identified as *Lates* from Eocene deposits in Fayum, Egypt (Weiler, 1929),

were referred to *Weilerichthys fajumensis* (Otero and Gayet, 1999b). Modern *Lates* is known from Lake Turkana (*L. niloticus* and *L. longispinis* Worthington, 1932) and is widespread throughout northern, eastern, and western Africa from Senegal to and including the Nile and Congo River Basins.

Percoidae incertae sedis

Semlikiichthys Otero and Gayet, 1999

Semlikiichthys rhachirhynchus (Greenwood and Howes, 1975)

Semlikiichthys cf. *S. rhachirhynchus*

KANAPOI MATERIAL. 3845, 4 first trunk vertebrae, 16 trunk vertebrae, 2 caudal vertebrae; 3846, 1 dentary, 1 first trunk vertebra, 5 trunk vertebrae, 4 caudal vertebrae; 3847, 4 dentaries, 1 first trunk vertebra, 9 trunk vertebrae, 3 caudal vertebrae; 3848, 1 vomer, 2 basioccipital, 4 first trunk vertebrae.

All material collected at Kanapoi is identical to drawings of *Semlikiichthys rhachirhynchus* (formerly *Lates rhachirhynchus* [Greenwood and Howes 1975] but renamed *S. rhachirhynchus* [Otero and Gayet, 1999a]; this author adheres to the original spelling [Greenwood and Howes, 1975] for “rhachirhynchus”), and is also identical to material collected at Lothagam, figured and described as *Semlikiichthys* cf. *S. rhachirhynchus* (Stewart, 2003). Full descriptions and photos of the extensive *Semlikiichthys* cf. *S. rhachirhynchus* material from Lothagam are found in the Lothagam volume (Stewart, 2003), where it is compared with the original drawings of *L. rhachirhynchus* (Greenwood and Howes, 1975).

In particular, the vomer recovered from Kanapoi is fully described in the Lothagam volume (Stewart, 2003), as it is the only vomer recovered from either Kanapoi or Lothagam which is almost identical to the type *S. rhachirhynchus* vomer (Greenwood and Howes, 1975), and is important in the naming of these fossils (*rhachirhynchus* means loosely “snout with spine”).

The Kanapoi elements establish a strong presence of *Semlikiichthys* cf. *S. rhachirhynchus* at Kanapoi.

As at Lothagam, *Lates niloticus* and *Semlikiichthys* cf. *S. rhachirhynchus* appear to have coexisted at Kanapoi. Both groups of fish seem to have attained large size, up to 2 m in length. This author has previously suggested (Stewart, 2001, 2003) that the presence of *Semlikiichthys* in the Turkana Basin resulted from exchange of faunas with the Lakes Albert and Edward Basins, the only other basins in which *Semlikiichthys* is known. Its reasonably common presence in Kanapoi further supports the suggestion of exchange. The identification of a palatine in Wadi Natrun Pliocene deposits probably referable to *Semlikiichthys* (Greenwood, 1972; Greenwood and Howes, 1975; discussed in Stewart 2001, 2003) also supports a more widespread faunal ex-

change within the Nile-linked systems, extending to the Egyptian Nile area.

Lates or *Semlikiichthys*

KANAPOI MATERIAL. 3156, 3 first trunk vertebrae, 1 caudal vertebra; 3845, 1 dorsal spine; 3846, 1 trunk vertebra; 3847, 1 maxilla fragment, 1 basioccipital, 1 pelvic spine; 3848, 1 basioccipital fragment, 4 vertebra fragments.

Perciformes Indeterminate

KANAPOI MATERIAL. 3156, 5 pelvic spines.

Pelvic spines are often difficult to distinguish between cichlids and *Lates/Semlikiichthys*. One pelvic spine appears to be more similar to those of cichlids, but not enough for positive identification. If so, it would be the only cichlid fossil recovered at Kanapoi. Cichlids are similarly rare at Lothagam.

PALEOECOLOGY

The Kanapoi fish fauna is characterized by two trophic components: large, piscivorous fish, in particular the polypterids, *Gymnarchus*, *Hydrocynus*, *Lates* (and probably *Semlikiichthys* by analogy), and the bagrid and clariid catfish; and medium to large molluscivores, including *Hyperopisus*, *Gymnarchus* (which is also a piscivore), *Sindacharax*, and possibly *Labeo*. Together with the numerous elements of the crocodile *Euthecodon* Fourteau, 1920, identified in the Kanapoi deposits, there was clearly much piscivory in this region of the Lonyumun lake (see, e.g., Tchernov, 1986, for details of *Euthecodon*). While *Euthecodon*'s diet probably consisted of the plethora of fish in the lake, the diet of the piscivorous fish must have included the numerous *Sindacharax*, *Hyperopisus*, and *Labeo* individuals, as well as smaller fish whose elements were not preserved. The near-absence of herbivorous fish, including *Barbus*, *Alestes*, and the large tilapiine cichlids is surprising. Most of these groups are common in modern Lake Turkana and the Nile system, and would be expected in the Pliocene lake. Certain absences may be explained by unfavorable environmental conditions (see **DISCUSSION AND SUMMARY** section). *Barbus* and the large tilapiine cichlids are generally scarce in African fossil deposits prior to the Pleistocene (Stewart, 2001).

The diversity and composition of taxa represented at Kanapoi is reminiscent of the modern Omo River Delta in northern Lake Turkana, which is inhabited, among other fish, by mormyriids, characoids, bagrids, clariids, and percoids. *Gymnarchus* and *Clarotes* in particular prefer delta regions (Lowe-McConnell, 1987). Many of the fish in the modern Omo River Delta region are intolerant of saline waters and therefore inhabit the delta and the lower reaches of the Omo River because they cannot tolerate the more saline Lake Turkana waters. Modern *Lates* is intolerant of deoxygenated waters, and the modern mormyriids are intolerant of saline waters. By analogy with the modern Omo Riv-

er Delta, Kanapoi waters may also therefore have been well-oxygenated and fresh.

The scarcity of fish such as *Protopterus*, *Polypertus* Saint-Hilaire, 1802, and *Heterotis* Ruppell, 1829, which were relatively common in the Nawata Formation at Lothagam, may signify an absence of vegetated, shallow backwaters or bays, as these are the type of habitats frequented by modern members of these taxa. The nearby Pliocene site of Eshoa Kakurongori contained numerous *Protopterus* toothplates, indicating a very different environment from Kanapoi.

DISCUSSION AND SUMMARY

Because the Kanapoi fish fauna comes primarily from one phase in the Kanapoi Formation—the lacustrine phase—there are no evolutionary or environmental transitions documented as was apparent through the Nawata and Nachukui Formations at the nearby Lothagam site. Nevertheless, the fauna alters some of the evolutionary and biogeographic interpretations made from the Lothagam fauna, as discussed below.

Most surprising is the comparison of the taxonomic composition from the Lothagam Muruogori deposits, Kanapoi deposits, and what the author has observed from the Ekora site deposits, all of which are presumed to derive from the Lonyumun Lake. The Muruogori deposits contain similar taxa to that at Kanapoi (Table 1), but also include two *Sindacharax* taxa—*S. deserti* and *S. greenwoodi*—and two *Tetraodon* Linnaeus, 1758, taxa—*T. fabaka* Hasselquist, 1757, and *Tetraodon* sp. nov., Stewart, 2003—which are common at Muruogori and at Ekora but which are completely absent from Kanapoi. Further, the most common *Sindacharax* species at Kanapoi—*S. mutetii*—is absent in the Muruogori Member and apparently in the Ekora fauna, although common in the Apak Member of Lothagam.

There are several possible explanations for this disparity in taxa between Kanapoi on one hand and Muruogori and Ekora on the other, which derive from the same lake. First, the different sites may represent different time intervals in the lake's history: the Ekora tetrapod fauna is said to be younger than that at Kanapoi (Maglio in Behrensmeyer, 1976), and the Muruogori Member may also be slightly younger than at Kanapoi. The "new" *Sindacharax* and *Tetraodon* taxa from Muruogori and Ekora may represent immigrants from a new inflow which was not present during Kanapoi deposition. The abundance of *S. mutetii* at both Kanapoi and in the Apak Member of Lothagam, which dates earlier than Muruogori and Ekora, may suggest an earlier deposition of the Kanapoi deposits, and a faunistic change between the Kanapoi, and Muruogori and Ekora waters. *Sindacharax mutetii* is completely absent from Muruogori and Ekora.

Alternatively, the Kanapoi and Muruogori and

Table 1 Fish taxa found in Mio–Pliocene deposits in Nawata, Apak, Muruogori, and Kaiyumung Members, Lothagam (Stewart, 2003) and Kanapoi (this report); see Feibel (2003a) and McDougall and Feibel (1999) for detailed information about the geochronology, geological formations, and members at Lothagam

	Nawata	Apak	Muruogori	Kaiyumung	Kanapoi
<i>Protopterus</i> sp.	+	+		+	
<i>Polypterus</i> sp.	+	+	+	+	+
<i>Heterotis</i> sp.	+	+	+		
<i>Hyperopisus</i> sp.		+	+	+	+
<i>Gymnarchus</i> sp.	+	+	+	+	+
<i>Labeo</i> sp.	?+	+	+	+	+
<i>Barbus</i> sp.		+		+	+
<i>Distichodus</i> sp.	+	+			+
<i>Hydrocynus</i> sp.	+	+	+	+	+
<i>Brycinus macrolepidotus</i>					+
Alestidae sp.	+			+	
<i>Sindacharax lothagamensis</i>	+	+			+
<i>S. mutetii</i>		+		+	+
<i>S. howesi</i>				+	+
<i>S. deserti</i>			+	+	
<i>S. greenwoodi</i>			+	+	
<i>Sindacharax</i> sp.	+	+	+	+	+
<i>Bagrus</i> sp.				+	
Aff. <i>Bagrus</i> sp.	+	+		+	
<i>Clarotes</i> sp.	+	+		+	
Bagridae/Claroteidae					+
<i>Schilbe</i> sp.	+				
<i>Clarias</i> or <i>Heterobranchus</i>	+	+		+	+
<i>Synodontis</i> sp.	+	+	+	+	+
<i>Lates niloticus</i>	+	+		+	+
<i>Lates</i> sp.	+	+	+	+	+
<i>Semlikiichthys</i>					
cf. <i>S. rhachirhinchus</i>	+	+	+	+	+
Cichlidae			+	+	
<i>Tetraodon</i> sp. nov.			+		
<i>Tetraodon</i> sp.			+	+	

Ekora deposits may represent different ecological zones in the Lonyumun Lake, with the “new” taxa restricted ecologically to local habitats and/or basins. Again the analogue of the modern Omo River Delta is appropriate here, with many taxa restricted to the delta region and not occurring in Lake Turkana proper.

A third alternative is that the field sampling was not extensive enough, and elements of the “new” taxa were not recovered at Kanapoi. This alternative seems less likely, as extensive screening was undertaken at all areas, and teeth of the “new” taxa should at least be somewhat represented at Kanapoi. Further, the *Tetraodon* toothplates are very robust and distinctive as fossils, and extensive surveying at Kanapoi should have recovered at least some toothplates, if this taxon had been present.

A third “new” taxon—cf. *Semlikiichthys rhachirhinchus*—was rare in earlier Lothagam deposits, but was common in the Muruogori Member at Lothagam, at Kanapoi, and at Ekora. This percoid apparently coexisted with *Lates niloticus*, which was also recovered in large numbers. Stewart

(2001) has reported that *S. rhachirhinchus* elements were also found in the Western Rift and probably at Wadi Natrun, suggesting interchange between the three systems. Otero and Sorbini (1999) have suggested that the genus *Lates* diversified in the fresh waters of Europe and Africa in the Miocene, from a Mediterranean origin. Further work is needed to clarify the relationships of *S. rhachirhinchus*.

In sum, the Kanapoi fauna is of considerable interest for several reasons. It has an unusual composition of mainly large piscivorous fish and medium to large molluscivores, and a scarcity of herbivorous fish. This composition is considerably different from that of modern Lake Turkana, which is much more evenly balanced between herbivores and piscivores. The scarcity of herbivores such as *Barbus* and the large tilapiine cichlids, common in the modern lake and the Nile River system, is particularly enigmatic.

While the Kanapoi fauna shares many taxa with the similarly aged Muruogori Member fauna from Lothagam and also from Ekora, it also shows some differences. The dominance of *Sindacharax mutetii*

at Kanapoi and in the Apak Member at Lothagam contrasts with its absence in the Muruogori deposits and at Ekora, as does the dominance of *S. deserti* and *Tetraodon* at Muruogori and Ekora, and their absence from Kanapoi and the Apak Member. Whether these disparities reflect ecological variants or chronological differences needs to be further studied.

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